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Caleigh Farrell
The University of Western Ontario

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RECONSTRUCTING PLIO-PLEISTOCENE PALAEO-ENVIRONMENTS

Caleigh Farrell

Abstract

Palaeo-ecological modeling is an important part of palaeoanthropology because major habitat changes are associated with significant evolutionary changes. To be able to derive an understanding of as to why Homo ergaster succeeded Homo habilis, Homo rudolfensis, and Paranthropus boisei we must understand the environmental factors that would have contributed to the evolutionary success of H. ergaster. In the analyses of extant and extinct fauna and flora from the Plio-Pleistocene and the microwear on hominid tooth remains we can develop an idea of what ecological niches these hominids may have exploited. However, what remains to be uncovered is how they were able to exist sympatrically with such evident dietary overlap. It is thus of utmost importance for palaeoanthropologists and primatologists to collaborate information in order to develop analogies between fossil hominids and extant primates. Potential analogies can be explored between gorillas, chimpanzees, bamboo lemurs and early hominids. Such analogies will aid in the reconstruction of Plio-Pleistocene environments that allow us to answer regarding whether ecological factors influenced initial hominid diversity and eventual extinction.

INTRODUCTION

The global climate changed drastically throughout the Plio-Pleistocene epochs, running from approximately five million years ago to 10,000 years ago. Formation of glacial ice caps left the African continent cooler, drier, and much more seasonal (Reynolds 2007:528). Hominids were greatly affected by these changes in Africa. Tectonic and volcanic activity as well as the appearance of palaeo-lakes rendered the landscape unrecognizable (Klein 1999:146). It is important to understand these environmental changes because they affect evolutionary patterns and processes tremendously. The co-existence of H. habilis, H. ergaster, H. rudolfensis, and P. boisei in East Africa during the Plio-Pleistocene marks an evolutionary puzzle. How is it possible that four bipedal hominids were able to live sympatrically in the Koobi Fora region of East Africa? Modeling palaeo-environments based solely on hominid fossil remains is difficult; there are simply too few fossil specimens to be able to derive an understanding of the significant environmental changes that occurred during early hominid existence. Therefore, we must turn our attention to other faunal remains that have been found in abundance, floral remains such as soil, volcanic deposits, and lastly our living relatives, the primates.

ANALYSIS OF FLORA AND FAUNAL REMAINS

The analysis of floral and faunal remains is of great importance in the reconstruction of palaeo-environments that existed during the Plio-Pleistocene. As seen in Vrba's analysis of African bovid speciation, a causal relationship is evident between climatic changes and macroevolution. A decline in temperature coincides with bovid speciation bursts and this occurs on a similar time scale to the emergence of the genus Homo. By implication there is a casual relationship between climate change and hominid evolution (Vrba 1985 cited in Foley 1994:275-276). As mentioned previously, the hominid fossil record is sparse, from bits and pieces of broken mandible and few complete crania, it is difficult to ascertain the climatic trends that influenced hominid

ecology. Therefore, in the analyses of other fossil specimen, which there is a relative abundance of, much useful information can be derived regarding the impact of climatic change on hominid evolution, as seen in Vrba (Vrba 1985 cited in Foley 1994:275-276). Furthermore, information relating to palaeo-environments and possible ecological niches that would have been available for our hominid ancestors to exploit could be derived.

Quinn *et al.* (2007), analyzes pedogenic carbonate isotope records from paleosols in relation to the spread of C4 grasses in Eastern Africa, in a recent article published by the Journal of Human Evolution, in order to develop greater clarity surrounding the ecological factors of early hominid evolution. Focusing on the 2.0-1.5 million years ago (Plio-Pleistocene epochs) time region, soil samples were analyzed from the Koobi Fora Formation, with emphasis on the upper Burgi, KBS, and lower Okote Members of the formation (Quinn *et al.* 2007:561). These formations are of specific importance to the study of early hominid evolution because from these layers hominid remains have been recovered. In particular interest to this topic is the KBS member in which all four hominids discussed here, P. boisei, H. rudolfensis, H. habilis, and H. ergaster, have been found, suggesting sympatric living.

In order to determine what types of environments characterized this locality Quinn *et al.* (2007) looked at the representations of C3 and C4 photosynthetic pathways, which have distinct differences in their carbon isotopic fractions. Woodland vegetation such as, trees, shrubs, temperate grasses utilize a C3 pathway that discriminates against the heavier and slower carbon 13 (13C). Tropical grasslands utilize a C4 pathway which includes more 13C into tissues. Savanna biomes are intermediate between C3 and C4 reflecting both a grassy and wooded vegetation (Quinn *et al.* 2007). Through the analysis of pedogenic carbonates, C3 and C4 carbon pathways, and carbon 12, information can be derived regarding the local environments of our hominid ancestors and other members of the faunal community. This study confirms the notion that the Pliocene and Pleistocene epochs were marked by an increase in aridity.

Furthermore, they conclude that the Koobi Fora Formation preserved a wide range of habitats. At Il Dura (a Koobi Fora Formation sub region), woodland savanna and thicket environments are expected to have occurred around and before 1.8 Ma due to low 13C values. Another sub region, Ileret, is believed to have had 40 to 60 per cent grassy vegetation, rendering it a savanna like locality. Finally, the Koobi Fora Ridge sub region would have consisted of a sparse savanna grassland environment with low-tree shrub (Quinn *et al.* 2007:567). What can be concluded from this study is that the Koobi Fora region consisted of a large mosaic of environments between 2.0-1.5 million years ago, with an evident shift towards C4 grasslands. The resulting extreme habitat fragmentation would have been further affected locally by, water availability, basin conditions, tectonics, volcanic activity, as well as by global climate cooling and drying. Additionally, said habitat fragmentation may have opened up additional niche spaces for hominids to live sympatrically at the time (Quinn *et al.* 2007:569-571).

Analysis of the geographic and temporal variation among mammalian taxa, both extinct and extant, can proved further insight in the discussion of environmental conditions that existed throughout hominid evolution (Reynolds 2007:528). The spotted hyena (Crocuta crocuta), the plains zebra (Equus burchellii) and the impala (Aepyceros melampus) are all evident in

abundance in the Plio-Pleistocene fossil record, unlike our hominid ancestors. Thus, they prove to be good indicators of possible geographic variations due to differences in climate. The Koobi Fora Region and Olduvai Gorge are the only two localities where all three species are present, dating to approximately 1.9 million years ago. These extinct and extant specimens were compared by craniodental measurements in order to compare temporal changes due to possible environmental shifts (Reynolds 2007:531).

Both the hyena and plains zebra differ in body size in response to climatic changes and geographic distinctions. A body size increase in colder temperatures has been observed in modern samples of the hyena, possibly to account for longer periods of fasting, enabling them to survive in more seasonal conditions. This observation follows a typical Bergmannian size cline, larger body sizes being found at colder temperatures (Reynolds 2007:543). Both the fossil spotted hyenas and plains zebras from Eastern Africa are significantly larger than their modern counterparts and show numerous size shifts, these results were not found to be replicated in South African specimen of the same species. There exists no dietary or behavioural overlap between these two taxa and therefore the assumption made that the shift in their morphology is due, in part, to broader climatic shifts, seems reasonable (Reynolds 2007:543-545). Although the same changes are not evident in analysis of the impala species, Reynolds (2007) argues that these results could be strongly influenced by the fact that the species is sexually dimorphic. The impala was however, strongly influenced by tectonic activity in Eastern Africa.

The significance of Reynolds (2007) study is that it provides evidence of more severe climate changes in East Africa, during the Plio-Pleistocene, than South Africa. Extreme seasonality in this region could lead to local extinction if a taxon does not exhibit dietary adaptations that allow the species to subsist on alternative food resources during food shortages. Seasonality does however create a multitude of ecological niches, which would offer opportunities for evolutionary innovation. These conclusions may be correlated with hominid evolutionary history in that one should expect a larger number of hominid species in Eastern Africa due to the availability of differing ecological niches but also a large number of extinctions (Reynolds 2007:546). Furthermore, it should be expected that the environmental changes in this region should be reflected in hominid morphology just as in hyenas, plains zebras, and bovids.

Thus far, it can be determined that the Plio-Pleistocene was marked by a rich mosaic of environments which offered habitat partitioning and thus multiple ecological niches for hominids to exploit. Due to the availability of a multitude of environments, hominids were able to exist sympatrically during the late Pliocene and early to mid Pleistocene.

DENTAL MORPHOLOGY, MICROWEAR AND EARLY HOMINID DIET

How did these hominids exploit these environments? To answer this question it is important to look at dental morphology and microwear on hominid tooth remains. Different dietary strategies will either morphologically change dental structure or leave lasting puncture marks or "scratches". Morphological adaptations in dental structure are exhibited in herbivores, carnivores, and omnivores. Each dietary strategy has developed its own morphological characters that aid in breaking down and digesting food. For example, herbivores have adaptations that attempt to reduce tooth wear; therefore, they have high crowns and reduced or missing

canines. Carnivores, have pronounced canine teeth and premolar and molar teeth with multiple cusps in order to sheer meat, called carnassial teeth. Lastly, omnivores exhibit a dental structure that is intermediary between herbivores and carnivores; they have multiple rounded cusps so that they can both sheer meat and grind plant like foods (Hodgetts 2007). Diet underlies many behavioural and ecological differences that separate mammalian species from one another; thus, it is of utmost importance for palaeo-anthropologists to examine these similarities and differences in palaeo-ecological modeling (Ungar *et al.* 2006:78).

Ungar *et al.* (2006) conducted a study examining the microwear features on fossil hominid teeth and compared them to a baseline consisting of five extant primate species (Cebus apella, Gorilla gorilla, Lophocebus albigena, Pan troglodytes, Papio ursinus), and two protohistoric human foraging groups (Aluet and Arikara). The protohistoric human foraging groups were included in this study because of conceivable similarities in subsistence strategies to that of early Homo (Ungar *et al.* 2006:82). This baseline represents a multitude of diet and feeding preferences and subsistence strategies and these differences are reflected in dental microwear. Individuals whose diet consists mainly of tough leaves exhibit more microwear (striations and scratches), while those that consume hard and brittle foods such as nuts at seeds, have larger microwear pitting. Species that consume mostly soft fruits tend to have an intermediate position in the number of scratches and pits evident in a tooth (Ungar *et al.* 2006:80).

By comparing hominid tooth remains to this baseline it is evident that early Homo (H. habilis and H. ergaster) had very few incidences of microwear pitting, rather they had features that correlate them with extant specimen that do not prefer fracture resistant foods. However, H. ergaster exhibited more microwear pits then H. habilis, inferring that they occasionally ate more brittle or tough food items, perhaps this was due to a lack of dietary specialization. H. habilis is thus in line with baseline groups such as the Arikara and G. gorilla who specialize on tougher foods such as leaves, woody plants, and occasionally animal tissues. H. ergaster, who exhibited more microwear pits, is analogous to the Aluet, P. troglodytes, and P. ursinus and therefore likely consumed tougher animal tissues and more fracture resistant foods (Ungar *et al.* 2006:85-86). This possible consumption of meat is positively correlated with improved hunting abilities, an expanded toolkit, increased social organizations, and larger brain mass which may have contributed to why H. ergaster was the evolutionary successor that arose out of this period (Ungar *et al.* 2006:79).

Fossil remains of H. rudolfensis are limited and thus determining dietary adaptations based on dental morphology is difficult. It is assumed that H. rudolfensis occupied a similar dietary niche to H. habilis with a heavier focus on folivory. Their large body size, larger cheek teeth with complex crowns, and thicker enamel imply a probable herbivorous diet.

The cranial morphology of P. boisei implies that their diet was completely vegetarian. The development of cranial structures, such as the sagittal crest and large zygomatic arches, infer that significant force was probable between the large upper and lower cheek teeth. Furthermore, the small size of their incisors and canines infer a preference for vegetal foods such as leaves and fruits (Klein 1999:214).

In sum, the sympatric hominids that existed during the Plio-Pleistocene in Eastern Africa occupied similar dietary niches. From Ungar *et al.*'s (2006) work it can be hypothesized that early Homo groups exploited similar foods; however, due to the

mass competition that would result, exploitation of difference fallback foods during times of food shortages is likely. H. habilis and H. ergaster appear to be opportunistic omnivores, eating meat when available. However, it seems likely that H. ergaster placed greater stress upon meat eating as seen by the higher percentage of microwear pits in their tooth enamel. H. rudolfensis and P. boisei exploited folivorous diets with possible fruit exploitation when available.

HOMINID ECOLOGY AND EXTANT PRIMATE ANALOGIES

It is known that there were four bipedal hominids with relatively similar diets coexisting in a mosaic of environments in the Koobi Fora region of East Africa during the Plio-Pleistocene. This would have resulted in extreme competition for food resources. This competition could have been ecologically sustainable in several ways. Firstly, the sympatric hominids may have eaten different foods or had different resources which they exploited as fall back foods when food was scarce. Secondly, their environments may have been temporally different. Temporally different environments can happen daily or seasonally leading the species to develop relatively opposite environments, for example, diurnal and nocturnal extant species. Lastly, they could exploit spatially different habitats (Rosenzweig 1999:68-75). Unfortunately, it is difficult to determine which one of these is applicable to early hominids from the fossil record alone. In order to over come this hurdle it is necessary that we look to sympatric extant primate species to derive information regarding how our hominid ancestors may have been ecologically divergent.

To start, I will examine the behavioural ecology of sympatric gorillas and chimpanzees and what implications these findings have on hominid ecology. By examining gorilla and chimpanzee ecological divergence in regards to diet, ranging patterns, and social organization, it is possible to make inferences as to how H. ergaster, H. habilis, H. rudolfensis, and P. boisei would have existed sympatrically. To reach any conclusions we must work under the assumption that both extinct and extant taxa obey the same ecological principles (in reference to body size, group size, and home range) and in doing so we are able to form analogies between species (Standford 2006:91). What is interesting about chimpanzee's and gorilla's sympatric existence is that they exploit similar food resources such as fruit, leaves, and shoots etc. but have different fall back foods during periods of food shortages. For example, chimpanzees will include invertebrates, honey, and mammalian prey in their diets, while gorillas focus on foods with much lower nutritional value such as leaves (Standford 2006:92-93). It is important to examine shared food preferences and sympatry between gorillas and chimpanzees in order to determine ecological constraints of such a relationship. Any conclusions derived from such studies would be beneficial in determining the relationships that existed between sympatric early hominids.

I propose that the ecological niches that P. boisei, H. habilis, and H. rudolfensis occupied were similar to that of gorillas and chimpanzees. In analyses of chimp and gorilla diet, a correlation is evident with those of the extinct hominids. By exploiting forest terrain, the hominids would have been safe from predators. Additionally, forests offer more ecological niches then grasslands and thus they would have had more partitioned habitats at their disposal. Furthermore, the three mentioned hominids all had arboreal climbing ability and they may have utilized different regions of the canopy and forest floor. In some situations,

it appears that chimpanzee's are ecologically dominant, over gorillas, in relation to access to food resources (Standford 2006:95). I hypothesize that H. habilis would have occupied this position as well, since both H. habilis and chimpanzees have exhibited use of modified tools and carnivory, the link seems probable.

The development of analogies between extinct and extant primate species cannot simply consist of those that link the great apes to our hominid ancestors, for this would be far too limiting. Although more genetically distant, the genus Hapalemur of Madagascar is important to study in establishing palaeo-ecological models. H. griseus (Lesser bamboo lemur), H. aureus (Greater bamboo lemur), and H. simus (Golden bamboo lemur) exist sympatrically in regions of Madagascar. Each one of these species is a year round bamboo specialist and they have adapted to exploit different regions of the giant bamboo (Tan 1999:547). These dietary decisions reflect ecologically constraining factors such as seasonal availability of food resources and intraspecific competition, as well as by their physiology and morphology. In areas where H. griseus, H. aureus, and H. simus occur sympatrically, extreme competition for resources results. The H. griseus has come to monopolize home ranges and has the broadest distribution throughout most parts of Madagascar. The remaining two populations have restricted distribution, occurring only in the south central part of the Eastern humid forests (Tan 1999:548). Because both the H. aureus and the H. simus live in such restricted regions, they are particularly vulnerable to the seasonal variability of the giant bamboo shoots.

It is important to examine the specialization of H. simus' diet. This species is greatly affected by the seasonal availability of food resources and their small population is likely a result of this (Tan 1999:558). A correlation between H. simus and early hominids can be derived in that as savanna grasslands began to spread out and environments became more seasonal, early hominid dietary specializations left them far too specialized, and therefore they suffered extinction due to their inability to adapt to changing climate.

Tan (1999) notes that the shared ancestry of the bamboo lemurs is likely to promote similarity in behavioural tendencies, ecology, morphology, and physiology. This is of particular interest to the study of early Homo lineage that existed during the Plio-Pleistocene. The behavioural, dietary, and morphological similarities between H. habilis, H. rudolfensis, and H. ergaster could have become too ecologically demanding which led to the eventual evolutionary success of H. ergaster and the extinction of the other. The dietary adaptation of bamboo lemurs reflects an ecological compromise that does not appear to have existed in early Homo.

The larger body sizes of the hominid fossil specimen may have been a large contributor to their lack of ability to be ecologically compromising. Body size is also positively correlated to range size. If H. ergaster followed a similar pattern, it would seem probable that their larger body and brain size lead them to monopolize the environment and spread out their home ranges because their food consumption demands were much greater than the other hominids. Dietary flexibility in the H. griseus further explains the larger home range and as we saw in analysis of H. ergaster dental remains, they exploited a more diverse diet than the other hominids (Tan 1999:553). I hypothesize that H. ergaster occupied similar ecological patterns as the H. griseus and eventually spread out and monopolized all other hominid species ecological niches, wiping them out.

In examining gorillas, chimpanzees, and bamboo lemurs we can derive an understanding of differential resource use and how Plio-Pleistocene hominids exploited similar ecological niches. Natural selection is in favor of niche partitioning and the fact that the East African hominids had such overlap could quite possibly have lead to their eventual extinction, excluding H. ergaster. If hominids follow the same ecological principles as all other mammalian taxa, sympatric species infer intraspecific competition will have played a central role in which lineage eventually succeeded the others (Standford 2006:92).

CONCLUSION

Through the process of reconstructing palaeo-ecological modeling palaeoanthropologists can derive valuable information regarding the ecology of our hominid ancestors. By looking at the zooarchaeological fossil record and floral remains, it is possible to determine the local environments that existed in Koobi Fora, East Africa during the Plio-Pleistocene, which proved to be a rich mosaic of habitats. Hominid tooth remains offered unique insights into the dietary specializations of H. ergaster, H. habilis, H. rudolfensis, and P. boisei. It appears that H. ergaster and H. habilis were opportunistic omnivores while H. rudolfensis and P. boisei maintained strict herbivorous diets. Through analogies formed between extant primates and early hominids, palaeoanthropologists can make inferences regarding possible environmental factors that existed during the Plio-Pleistocene that allowed early hominids to live sympatrically. Furthermore, the ecological factors which may have aided H. ergaster's relative success in evolutionary history might also be uncovered. It is of utmost importance that future research collaborates with primatologists in a bid to reconstruct the palaeo-ecology of Plio-Pleistocene hominids.

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